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# Morphology and hosts of three *Striga* species (*Scrophulariaceae*) in Botswana

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**Summary** : *Striga asiatica* (L.) Kuntze, *Striga gesnerioides* (Willd.) Vatke and *Striga bilabiata* (Thunb.) Kuntze were studied in the field and in pot experiments in Botswana. Morphological variation within *S. asiatica* appears to be due to environmental rather than genetic factors. The calyx of *S. asiatica* can vary considerably with 11 to 16 ribs on calyces of 5 to 9 teeth. New ribs may develop as the capsule matures. Distinct morphotypes of *S. gesnerioides* are common in Botswana and four are described using internode length and hosts as criteria. *Striga bilabiata* is strongly autogamous. Pollination is similar to that described earlier for *S. asiatica* except that the stigmatic surface in *S. bilabiata* extends down the adaxial surface of the style. Crosses among three species were attempted but no capsules were produced suggesting genetic isolation. Crosses of *S. asiatica* × *S. asiatica* and *S. gesnerioides* × *S. gesnerioides* were always fertile.

**Résumé** : *Striga asiatica, S. gesnerioides* et *S. bilabiata* ont fait l'objet d'études de terrain et d'expérimentations en pots, au Botswana. La variation à l'intérieur de *S. asiatica* est à attribuer aux facteurs d'environnement plus qu'aux facteurs génétiques. Le calice de *S. asiatica* peut avoir 5 à 9 dents, et porter 11 à 16 nervures ; des nervures supplémentaires peuvent apparaître au cours de la maturation de la capsule. A l'intérieur de *S. gesnerioides*, on observe communément, au Botswana, des morphotypes différents ; quatre sont décrits ici en utilisant comme critères la longueur des entrenœuds et les hôtes. *S. bilabiata* est fortement autogame ; la pollinisation est similaire à celle décrite auparavant chez *S. asiatica*, sauf que la surface stigmatique, chez *S. bilabiata*, s'étend vers le bas sur la face adaxiale du style. Des croisements entre ces trois espèces ont été tentés, mais il n'en est résulté aucune capsule, ce qui suggère une isolation génétique. Des croisements de *S. asiatica* × *S. asiatica* et de *S. gesnerioides* × *S. gesnerioides* furent toujours fertiles.

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## INTRODUCTION

Species of *Striga* are the most serious parasitic weeds in Africa. *Striga hermonthica* is of tremendous importance in the Sahelian region as a pathogen of sorghum and millet. In West Africa, *S. gesnerioides* is a factor in yield reduction of cowpeas (Musselman, 1980). In southern Africa the most serious species is *S. asiatica* which attacks maize, sorghum and millet. The witchweeds of Botswana have recently been reviewed (RICHES, 1984; MUSSELMAN & RICHES, 1985) but little other work on *Striga* in Botswana has been done. The purpose of this paper is to report on detailed morphological studies, breeding relationships, and hosts of three widespread species : *Striga asiatica* (L.) Kuntze, *S. gesnerioides* (Willd.) Vatke, and *S. bilabiata* (Thunb.) Kuntze. This is part of an overall effort to develop a broad based phenetic taxonomy of African *Striga* species.

Various control methods have been investigated; hand-weeding, application of herbicide, fumigation of soil with stimulants to produce suicidal seed germination, crop rotation with stimulant-producing non-hosts, and application of high levels of nitrogen but such methods are unlikely to be appropriate for resource-poor small farmers in Botswana and other underdeveloped areas (MUSSELMAN & RICHES, 1985). A more economic approach would be to distribute resistant host seed to such farmers. Accordingly, many research efforts in *Striga* control are directed at developing crop lines with resistance or tolerance to the parasite (e.g. RAO et al., 1981). These efforts are, however, contingent on further research on *Striga* biology and genetics. Information is needed on the possible importance of genetic interchange in the breakdown of resistance. For example, in Botswana, there is the opportunity for outbreeding in communities where several *Striga* species occur together and flower simultaneously. However, it is not known if genetic interchange occurs. Furthermore, different sources of resistance may be required if parasite populations are found to differ genetically from one area to another.

## MATERIALS AND METHODS

*S. asiatica* and *S. gesnerioides* for use in experimental crosses and morphological observations were grown in pots sunk in soil in the field at Agricultural Research Station near Gaborone Botswana. (Lat. 24°34′ S, Long. 25°57′ E, Alt. 994 m). Detailed procedures are in RALSTON et al. (in preparation). In trial 1 four accessions of *S. asiatica* seed collected from various parts of Botswana were used to infest soil in which *Sorghum bicolor* and *Digitaria smutsii* were grown as hosts. In trial 2 seed of *S. asiatica* collected from sorghum, maize and pearl millet (SA9, 10, 11) was used to infest soil sown with sorghum and pearl millet as hosts. Parasite seed used are recorded Appendix one.

## EXPERIMENTAL CROSSES

Once plants of *S. gesnerioides* (parasitising *Indigofera daleoides*) were flowering at the same time as plants of *S. asiatica* (parasitising sorghum or millet), reciprocal crosses were attempted between and amongst species. Pollen was collected in the morning from the staminate parent onto a microscope slide and smeared onto the stigma of the pistillate parent. Pistillate parents were always first emasculated by removal of the corolla tube and epipetalous androecium before dehiscence of anthers occurred. Crosses were made as in Table 1 between *S. asiatica* and *S. gesnerioides*. Crosses were also made between *S. asiatica*.

Successful crosses were scored by enlargement of the capsule due to seed production. In addition, reciprocal crosses were made between wild plants of *S. bilabiata* growing at Nxai Pan (Fig. 1) and potted specimens of *S. asiatica* and *S. gesnerioides* (Table 2).

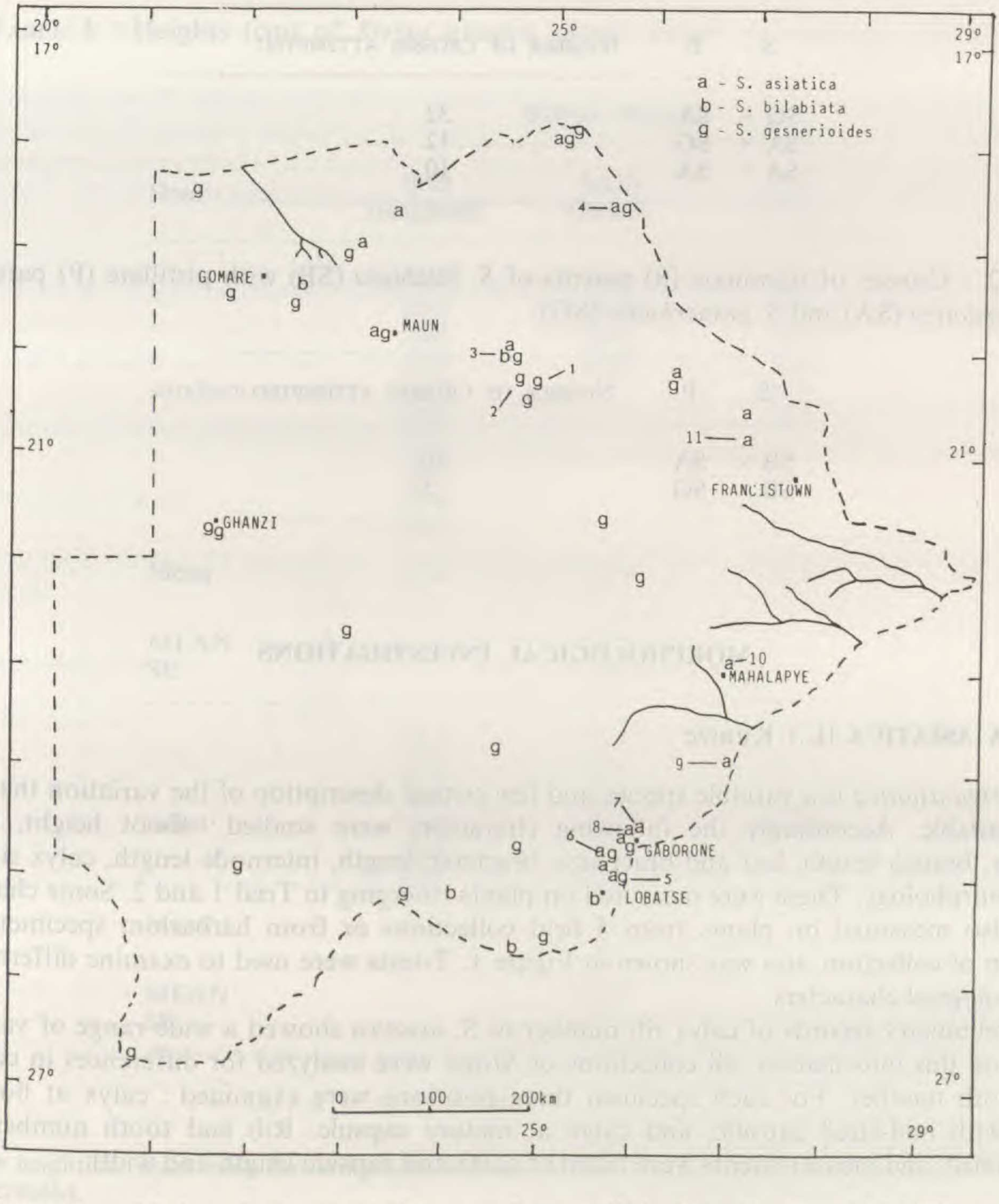


FIG. 1. — Location of **Striga** collection sites in Botswana. Sources : Herbarium collections and field observations by authors. Major collection sites : 1, Maun-Nata 1 ; 2, Maun-Nata 3 ; 3, Kanyu ; 4, Pandamatenga ; 5, Otse ; 6, Manoko ; 7, Mma-mashia ; 8, Sebele ; 9, Ramatlabaki ; 10, Mahalapye ; 11, Marapong.

TABLE 1 : Reciprocal crosses of staminate (S) and pistillate (P) parents of *S. asiatica* (SA) and *S. gesnerioides* (SG).

| S | P | NUMBER OF CROSSES ATTEMPTED |
|---|---|---|
| SG × | SA | 32 |
| SA × | SG | 12 |
| SA × | SA | 10 |

TABLE 2 : Crosses of staminate (S) parents of *S. bilabiata* (SB) with pistillate (P) parents of *S. asiatica* (SA) and *S. gesnerioides* (SG).

| S | P | NUMBER OF CROSSES ATTEMPTED |
|---|---|---|
| SB × | SA | 10 |
| SB × | SG | 5 |

## MORPHOLOGICAL INVESTIGATIONS

### STRIGA ASIATICA (L.) Kuntze

*Striga asiatica* is a variable species and few critical description of the variation that exists are available. Accordingly the following characters were studied : shoot height, branch number, branch length, leaf and bract size, bracteole length, internode length, calyx size, and floral morphology. These were measured on plants emerging in Trial 1 and 2. Some characters were also measured on plants from 5 field collections or from herbarium specimens. The location of collection sites was shown in Figure 1. T-tests were used to examine differences in morphological characters.

Preliminary records of calyx rib number in *S. asiatica* showed a wide range of variation. Based on this information, all collections of *Striga* were analyzed for differences in calyx rib and tooth number. For each specimen three positions were examined : calyx at flowering, calyx with mid-sized capsule, and calyx at mature capsule. Rib and tooth numbers were determined, and measurements were taken of calyx and capsule length and width.

### POT CULTURE

#### Plant height

The height of *Striga* shoots was not found to differ among *S. asiatica* sources or hosts in Trial 1. In Trial 2, however, shoot height was significantly greater (P = 0.01) in pots of sorghum, where mean height was 25.3 cm, compared with a mean of 18.9 cm in pots of millet (Table 3).

TABLE 3 : Heights (cm) of *Striga asiatica* shoots grown on sorghum and millet.

| | STRIGA SOURCE | | |
|---|---|---|---|
| HOST | SA9 (sorghum) | SA10 (maize) | SA11 (millet) |
| sorghum | 31.0 | 25.0 | 21.0 |
| | 27.2 | 26.0 | 22.2 |
| | 28.4 | 26.2 | 23.0 |
| | 27.8 | 22.9 | 21.0 |
| | 28.0 | | 20.5 |
| | 27.0 | | 23.2 |
| | 27.5 | | |
| | 28.2 | | |
| | 26.0 | | |
| | 24.5 | | |
| Mean : | 27.6 | 25.0 | 21.8 |
| MEAN : | | 25.3 | |
| SE : | | 0.7 | |
| millet | 14.5 | 12.5 | no growth |
| | 17.5 | 28.5 | |
| | 20.8 | 18.5 | |
| | 16.0 | 19.0 | |
| | 15.5 | 15.5 | |
| | 19.8 | 28.5 | |
| Mean : | 17.3 | 20.4 | |
| MEAN : | | 18.9 | |
| SE : | | 1.5 | |

t = 7.01 ; df = 30; P = 0.001.

Greater height can infer more flowering area and seed production, provided internode length is not also increased.

**Branch number**

Branch number refers to the number of nodes from which branches arise on the main stem of a *Striga* shoot. Generally, branches occur in pairs, although triplets may be found. On shoots where triplets occur at branch nodes, they also appear at floral nodes.

No significant differences could be found in the number of branches per *Striga* shoot between host or *Striga* source for any of the trials.

**Branch length**

In Trial 1, total length of branches of *Striga* shoots was found to be greater (non-significant, P = 0.1) on those shoots emerged in pots of sorghum than on those emerged in pots of *Digitaria* (Table 4). The mean total branch length was 93.1 cm in pots of sorghum and 40.4 cm in pots of *Digitaria*.

TABLE 4 : Total length of branches on shoots of *S. asiatica* growing on sorghum or *Digitaria* in Trial 1.

| | HOTS | |
|---|---|---|
| | sorghum | *Digitaria* |
| | 218.4 | 0 |
| | 195.0 | 29.0 |
| | 62.6 | 94.6 |
| | 88.0 | 12.0 |
| Total | 27.2 | 25.0 |
| branch | 191.2 | 80.0 |
| length | 17.0 | 42.0 |
| (ca.) | 131.0 | |
| | 184.0 | |
| | 65.4 | |
| | 64.0 | |
| | 138.0 | |
| | 71.0 | |
| | 105.0 | |
| | 67.0 | |
| | 27.0 | |
| | 69.6 | |
| | 16.0 | |
| Mean : | 93.1 | 40.4 |
| SE : | 16.1 | 13.2 |

t = 1.9; df = 23; P = 0.1.

In Trial 3, no significant differences were found in branch length between witchweeds grown on sorghum and those on millet, nor were any found between *Striga* sources in all three of the trials. The number and length of branches of a *Striga* plant are pertinent to its vigor. A higher number of branches, together with a greater total length, produces more seed, which enables the parasite to infest an area very quickly. In terms of the survival of the species, such plants can be considered more successful, and sorghum, therefore, can be considered a better host than *Digitaria*.

**Leaf and bract size**

Size dimensions were measured from the largest leaf of bract per shoot, as an indicator of maximum growth under the given conditions. Therefore, the means presented do not represent an average over a single plant, rather, they are for use in comparing growth between treatments. Most leaves and bracts on a single *Striga* plant will be smaller.

Maximum width of leaves and bracts of *S. asiatica* did not vary significantly for any treatments.

Maximum length of leaves and bracts was also found to be consistent across host and SA seed source in Trials 1 and 2. However, in Trial 3, this parameter was found to be significantly ($P = 0.05$) greater in sorghum pots than millets pots, where mean length was 40.3 cm and 32.3 cm, respectively. Difference in size occurred only in those leaves and bracts on the main stem; leaves and bracts on branches achieved similar sizes across all treatment.

**Bracteole length**

Bracteole length of shoots of *S. asiatica* measured from 3-5 mm, on average, for all treatments.

**Internode length**

The internode length of shoots of *S. asiatica* at maturity ranged approximately from 15-20 mm. No differences were found among treatments.

**Calyx size**

Size of the calyx was found not to vary significantly among treatments. The average length was 7 mm.

**Floral morphology**

Flower color ranged from deep scarlet to bright red to an orange shade. Variation did not occur in any predictable manner. The corolla tube was 10-12 mm long, on average, with a maximum of 15 mm found. One upper lobe averaged 4-5 mm across. Three lower lobes averaged 4 mm in width, by 5-6 mm length. Differences in flower size were random across treatments.

FIELD COLLECTIONS

Morphological records to 10 plants collected at random from each site. Nine herbarium sheets, at the Botswana National Herbarium, were also examined; morphological characters were consistent with the findings in our field collections.

**Shoot height**

*Striga* plants collected from south-eastern Botswana from sorghum plants in farmers fields at Manoko, Mma-mashia, and Otse (see Figure 1) were found to achieve comparable heights. Specimens examined from the three sites had a mean height of 18.4 cm (Table 6). This figure is significantly (P = 0.001) less than the mean recorded for plants in the above trials (23.35 cm across all treatments except millet), possibly due to the lower amount of moisture available to plants in rain-fed fields.

TABLE 6 : Heights of *Striga asiatica* shoots parasitising Sorghum collected from Manoko, Mma-mashia, Otse, and Pandamatenga, and collected from grassland at Pandamatenga.

| | COLLECTION AREA | | | | |
|---|---|---|---|---|---|
| | Manoko | Mma-mashia | Otse | Pand. sorghum | Pand. grasslands |
| | 27.0 | 25.0 | 18.7 | 34.5 | 47.5 |
| | 27.0 | 25.0 | 18.7 | 34.5 | 47.5 |
| | 13.0 | 15.5 | 21.0 | 33.5 | 28.7 |
| | 16.4 | 26.5 | 14.0 | 22.5 | 40.3 |
| | 16.8 | 16.5 | 10.0 | 31.0 | 32.5 |
| Heights | 22.7 | 21.0 | 16.4 | 30.0 | 37.0 |
| (ca.) | 12.6 | 12.6 | 15.0 | 37.0 | 30.0 |
| | 14.5 | 31.0 | 20.5 | 37.5 | 44.5 |
| | 21.2 | 24.0 | 17.7 | 28.6 | 42.0 |
| | 20.5 | 21.0 | 10.0 | 37.0 | 36.0 |
| | 20.2 | 18.4 | 16.0 | 30.5 | 39.5 |
| | 14.3 | | | | |
| Mean : | 18.1 | 21.1 | 16.0 | 32.2 | 37.8 |
| MEAN : | | 18.4 | | | 35.0 |
| SE : | | 0.9 | | | 1.3 |

t = 10.63 ; df = 49 ; P = 0.001.

Similarly, a response to available moisture is suggested in *Striga* specimens collected from the Pandamatenga area in northern Botswana. Rainfall for the season was considerably higher around Pandamatenga — 1000 mm, compared with a mean of 321.9 mm around the southeastern area — and the soil has a greater clay content. Accordingly, both host and *Striga* plant, relieved of drought stress, are able to grow more vigorously. *Striga* plants collected from farmers fields and grasslands at Pandamatenga grew to a mean height of 35 cm (significantly larger than south-eastern collections at P = 0.001).

**Branch number**

No difference was found in the number of branches on *Striga* shoots collected off sorghum from farmers fields at Manoko, Mma-mashia, Otse, and Pandamatenga. However, branch number was significantly (P = 0.001) lower on *Striga* shoots collected from grasslands (Table 7). At Pandamatenga, the mean branch number of grassland plants was 0.9, compared with a mean of 3.5 for specimens from farmers fields.

TABLE 7 : The number of branching nodes per *Striga* shoot of specimens parasitising Sorghum collected from Manoko, Mma-mashia, Otse, and Pandamatenga and collected from grassland at Pandamatenga.

| | COLLECTION AREA | | | | |
|---|---|---|---|---|---|
| | Manoko | Mma-mashia | Otse | Pand. sorghum | Pand. grasslands |
| No. of branch nodes | 3 | 6 | 4 | 4 | 2 |
| | 2 | 2 | 6 | 4 | 0 |
| | 3.5 | 4 | 5.5 | 1 | 1 |
| | 5 | 3 | 3 | 5 | 0 |
| | 4 | 4 | 2.5 | 1 | 1 |
| | 4 | 3 | 3 | 4.5 | 1 |
| | 2.5 | 3 | 0.5 | 2.5 | 0 |
| | 4 | 7 | 6.5 | 6 | 1.5 |
| | 2 | 4 | 3 | 5 | 1 |
| | 4 | 2 | 3 | 2 | 1.5 |
| | 6 | | | | |
| Mean : | 3.6 | 3.8 | 3.7 | 3.5 | 0.9 |
| SE : | 0.4 | 0.5 | 0.6 | 0.6 | 0.2 |

t = 4.33 ; df = 18 ; P = 0.001.

**Branch length**

Branch length was also found to vary significantly (P = 0.001) between *Striga* specimens collected from sorghum and grassland at Pandamatenga (Table 8). The mean of the total branch length for shoots growing on sorghum was 130.4 cm, while the mean for shoots growing in grassland was 21.0 cm.

TABLE 8 : Total branch length per *Striga* shoot of specimens parasitising sorghum collected from Manoko, Mma-mashia, Otse, and Pandamatenga, and collected from grassland at Pandamatenga.

| | Manoko | Mma-mashia | Otse | Pand. sorghum | Pand. grassland |
|---|---|---|---|---|---|
| | 60.0 | 108.0 | 37.0 | 157.0 | 28.6 |
| | 32.0 | 14.0 | 115.0 | 126.0 | 0.0 |
| | 44.0 | 144.0 | 57.0 | 70.0 | 13.0 |
| Total. | 72.0 | 60.0 | 33.0 | 180.0 | 0.0 |
| branch | 81.0 | 60.0 | 42.0 | 16.0 | 46.0 |
| length | 35.4 | 19.0 | 52.0 | 238.0 | 34.0 |
| (ca.) | 24.0 | 70.0 | 20.0 | 116.0 | 0.0 |
| | 86.0 | 142.0 | 120.0 | 194.0 | 38.0 |
| | 13.0 | 38.0 | 35.0 | 176.0 | 2.0 |
| | 70.0 | 30.0 | 54.0 | 31.0 | 48.0 |
| | 144.0 | | | | |
| Mean : | 60.1 | 68.5 | 56.5 | 130.4 | 21.0 |
| MEAN : | | 61.7 | | | |
| SE : | | 7.0 | | 22.8 | 6.3 |

Pand. farm v. grass : t = 4.58 ; df = 18 ; P = 0.001. SE farms v. Pand. farm : t = 3.86 ; df = 39 ; P = 0.001. d.

Furthermore, significant (P = 0.001) differences existed in branch length between the northern and south-eastern farm collections; means were 130.4 cm and 61.7 cm, respectively, indicating that branch length, as well as shoot height, may be greater under adequate moisture.

**Leaf and bract size**

*Striga* leaves and bracts along the main stem were widest on plants growing on sorghum in Pandamatenga. With a mean maximum width of 3.35 mm, these plants outgrew the northern grassland types (P = 0.001), with a mean width of only 1.7 mm, and the south-eastern specimens (at P = 0.05), which has a mean width of 2.6 mm.

Maximum length of leaves and bracts along the main stem was also greatest on Pandamatenga *Striga* growing on sorghum. The mean for these specimens was 39.5 mm. Mean length of leaves and bracts for the grassland type was 27.0 cm. The three south-eastern farm collections has a mean maximum leaf length of 29.0 cm, significantly (P = 0.001) less than the Pandamatenga farm type.

Leaves and bracts growing on branches also varied in length among field collections. Maximum length was observed on Pandamatenga farm-type *Striga* with a mean of 23 cm. South-eastern farm collections had a mean branch leaf length of 18.5 cm (significantly less at P = 0.05), and the grassland *Striga* plants achieved a length of only 6.3 cm, if branching occurred at all.

Maximum width of leaves and bracts on branches was not found to differ significantly between collections.

### Bracteole length

This character was also similar between *Striga* grown in trials and those found in fields in the south-eastern area. Bracteole length of specimens from Manoko, Mma-mashia, and Otse was 3-5 mm. *Striga* from the Pandamatenga grassland developed bracteoles in this range, as well. Yet, the farm collections from Pandamatenga developed bracteoles 6-10 mm in length.

### Internode length

As in the trial plots, the internode distance of *Striga* plants growing in farmers' fields in the south-eastern area averaged about 15-20 mm. Both collections from Pandamatenga, however, had internode lengths of 30-35 mm. The longer distance between nodes indicates that the generally enhanced growth of *Striga* in the northern area is largely due to elongation.

### Calyx size

The mean calyx length of Pandamatenga collections was 7.9 mm. This figure is comparable with the mean calyx length in trial specimens. However, south-eastern field collections were found to have mean calyx lengths of 6.06 mm, which were significantly ($P = 0.001$) lower.

### Floral morphology

Variation in coloration was similar for trial flowers. A yellow-flowering type from Mogobane, in the South-east District is in the *Botswana National Herbarium (no. 1801)*, but the authors did not observe any yellow flowers in the numerous field stands observed.

Flower size did not vary appreciably from trial findings.

### Calyx investigation

The examination of calyces for each *S. asiatica* collection showed enormous variability in rib and tooth number. The most common combination was 11 ribs on a calyx with five teeth, yet the range was found to be 11-16 ribs on calyces with 5-9 teeth. The arrangement was quite variable even within a single plant. The one exception to this variability was found in the Pandamatenga collection from grassland; virtually all calyces examined had 11 ribs and 5 teeth.

The investigation of three calyx locations on a single plant, at flowering, at mid-size capsule, and at mature capsule, provides insight into the temporal development of the calyx. A general trend seemed evident where 5 teeth and 11 ribs would occur at flowering, progressing to as many as 9 teeth and 16 ribs on calyces encasing mature capsules. The calyces with a greater number of teeth were generally larger, as often were the seed capsules. It is possible, therefore, that *Striga* expands its calyx size by increasing rib number to protect developing seed capsules.

The 5-toothed, 11-ribbed calyx was found to alternate a rib terminating a tooth with a rib terminating a sinus, except in the location opposite the stem, adjacent to the bract, where two ribs were present in the sinus. Where more than five teeth were found, it appeared that one or more sinus ribs had elongated. No particular rib position was favoured; all arrangements of ribs terminating teeth or sinuses could be found.

During investigation, the possible development of new ribs could be observed. Ribs appeared to split longitudinally, pull away from each other and increase rib number. Often, one sinus rib appeared to be splitting off on either side, yielding three ribs, and a new tooth seemed to develop as the centermost rib elongated. Such a process would have to be monitored over time to be confirmed. In other instances, teeth ribs appeared to split off to form new sinus ribs.

The uniformity in the Pandamatenga grassland collection may reflect that seed capsules on these plants only reach a certain size adequately protected by a calyx with five teeth and eleven ribs. In this case, one would expect that the mature capsule size for this collection would be smaller than for other collections. However, such findings were not always significantly different (Table 5).

TABLE 5 : Length of mature seed capsules of five field collections of *S. asiatica*.

| | COLLECTIONS AREA | | | | |
|---|---|---|---|---|---|
| | Manoko | Mma-mashia | Otse | Pand. sorghum | Pand. grasslands |
| Length (cm) | 5.0 | 4.0 | 3.0 | 4.0 | 3.0 |
| | 4.5 | 5.5 | 5.0 | 5.5 | 3.5 |
| | 6.0 | 4.0 | 5.0 | 4.0 | 4.0 |
| | 4.0 | 5.0 | 6.5 | 3.5 | 4.0 |
| | 6.0 | 5.5 | 6.0 | 5.0 | 4.5 |
| | 6.0 | 5.0 | 6.0 | 4.0 | 4.0 |
| | 4.5 | 4.0 | 6.0 | 5.0 | 4.0 |
| | 6.0 | 4.0 | 4.0 | 6.0 | 4.0 |
| | 6.0 | 4.0 | 3.0 | 3.5 | |
| | 6.0 | 5.5 | | | |
| | 4.0 | | | | |
| Mean | 5.3 | 4.7 | 4.9 | 4.2 | 3.9 |
| SE | 0.9 | 0.7 | 1.3 | 0.9 | 0.4 |

It was common to find two or three ribs terminating a calyx tooth, a situation that is not treated in *Striga* keys. In fact, the large number of different rib and tooth arrangements made it a questionable character for use in keys.

**STRIGA GESNERIOIDES** (Willd.) Vatke

*S. gesnerioides* from only two sources developed on the hosts used in trials, as shown below :

| | *Striga* source (Host) | | | |
|---|---|---|---|---|
| | SG1 (*Indigofera*) | SG2 (*Tephrosia*) | SG3 (*Tephrosia*) | SG4 (not recorded) |
| HOST | | | | |
| Tobacco Tv133 | — | + | — | — |
| *Indigofera* | + | — | — | — |

+ for emergence

In Trial 1, SG1, collected from *Indigofera*, only attacked *Indigofera* emerging in four of five pots. Examination of the roots of potential hosts at the termination of the trials indicated that no other parasite development had occured. SG2, collected from *Tephrosia sp.*, showed weak development on tobacco, but not *Indigofera*. In a preliminary pot trial, the parasite emerged 162 days after the tobacco was sown and flowered 10 days following emergence. In another pot trial, emergence occured in one pot of tobacco only, at 161 days. Growth of *S. gesnerioides* after emergence on tobacco was, however, poor. Plants grew to no more than 40 mm high, produced up to four flowers and died back. Plant morphology was, however, similar to the source material collected from *Tephrosia* (fleshy green stems with short internodes).

In the latter pot trial, haustoria were found on tobacco roots in several pots when tipped out and discarded after 191 days. On some haustoria, shoot initials could also be observed, yet emergence occured in only the one pot.

Although, as a species, *S. gesnerioides* has a wide host range, specialized strains which are host-specific have been reported by a number of authors. WILD (1948) demonstrated that while *S. gesnerioides* on tobacco could be germinated by cowpea root exudate, no attatchment of the parasite to cowpea occurs. Further evidence that certain strains of *S. gesnerioides* will only parasitize the host from which they are collected was provided by MUSSELMAN & PARKER (1981). In our trials only one variety of tobacco was used, but tentatively, the *Indigofera* form appears specific to *Indigofera*. Likewise, SG3 may be specific to *Tephrosia*. A germination test showed this seed batch to be viable at approximately 7 %. Insufficient seed prevented a test on SG4. A broader host range is indicated, however, for SG2 (ex. *Tephrosia*), because it parasitized, albeit weakly, tobacco. This is the only crop host of *S. gesnerioides* in southern Africa. In Zimbabwe, the species has been reported as a problem on tobacco in limited areas. *Tephrosia* spp. have also been collected as hosts in Zimbabwe (WILD, 1948).

### Morphology

In view of the limited emergence of *S. gesnerioides* in the trials, comments on the morphology of the species in Botswana will be restricted largely to field collections from 14 sites. With some notable exceptions, e.g. Maun-Nata Road sites 1 and 2, the density of *S. gesnerioides* found at a particular location tends to be low. The following records refer normally to 4-5 mature plants per site and should, therefore, be seen as largely descriptive. However, a presentation of the range of dimensions of *S. gesnerioides* seen throughout Botswana does provide a useful characterization of species for comparison with collections from other parts of Africa. This section may provide some insight into which diagnostic characters used elsewhere hold up and which need modification in order to include the range of variation seen in Botswana in a workable description of the species as a whole. Details of collection sites are given in the Appendix.

Combinations of key characters are then used to prepare tentative morphotypes of the species seen to date (this being without doubt the most variable and widespread member of the genus in Botswana).

#### Appearance

Collections range from tall, slender stems with long internodes to rather succulent short plants with closely packed nodes. Most plants varied from pale to dark green. Some collections, e.g. Kanyu (sheet 26), had totally red stems and foliage.

#### Primary haustorium

Plants of *S. gesnerioides* usually have a large, tuberous primary haustorium. On plants from Maun-Nata site 2, the haustorium is particularly large at up to 2 cm in diameter.

#### Shoot height

The tallest plant (*Botswana National Herbarium No. 1089*, Kgale mountain) is the only specimen measured over 30 cm. Mean heights of twelve collections investigated ranged from 8.2-24.3 cm; seven sites included individuals of over 17.5 cm and three of over 20 cm.

Although host and environment may influence parasite growth in a similar way to *S. asiatica*, as evident by the poor growth of SG2 on tobacco, height does seem associated with other characters, including — not surprisingly — internode length, but, more importantly, succulence and flower colour.

#### Branch number and position

Considerable variation in branching pattern was noted among collections. While at any site specimens could be found unbranched or with multiple stems, the positions of the branches appear related to other characters, in particular, height and flower colour. Six collections included specimens with 10 or more branches; the maximum recorded was 29.

Position of branches varied from all arising below ground or at ground level with the shorter, more succulent types, to branches arising off the main stem up to 8.5 cm above ground for taller types.

**Branch length**

Collections characterized by smaller, succulent specimens tended to have fairly short branches up to 8 cm. Elsewhere, branch length reached 18.5 cm.

Six collections included individuals with branches greater than 7.5 cm.

**Leaf and bract size**

All specimens of *S. gesnerioides* investigated had scale-like leaves appressed to the stem. Maximum leaf size of 4-12 mm long, by 1-4 mm wide was found on tall, non-succulent plant types, collected south of Gumare, western Ngamiland (sheet 35). Elsewhere, leaf dimensions were within the range of 1-8 mm long, by 1-4 mm wide.

In six collections, bract length was in the range of 5-8 mm. One collection from Kanyu (sheet 25), however, had smaller bracts at 3-4 mm, while length ranged from 5-10 mm for sheet 35.

**Bracteole length**

Across all collections, bracteole length varied from 3-7 mm. Three collections, Maun-Nata Road site 1 and site 2, and Makgadikgadi (sheets 21, 22, and 36, respectively), included specimens with bracteoles over 5 mm long.

**Internode length**

Internode length is a further character which is closely related to plant succulence, height, and, to some extent, flower color. Generally, internodes are shorter between floral nodes than between leaf or branch nodes. It is not unusual, however, in *S. gesnerioides* to find floral nodes at ground level. The succulent, yellow-flowered type from Maun-Nata site 2 (sheet 22), for example, included specimens of this type. Floral internodes in this collection and other short internode types, e.g. sheets 21, 22, 24, and 36, are in the range of 2-7 mm.

Eight collections included specimens with vegetative internodes over 10 mm. Four had internodes in excess of 20 mm. These long internode types tend to be non-fleshy and have light pink flowers. Floral internodes on such specimens, e.g. sheets 26, 27, 28, and 35, regularly reach up to 20 mm.

**Calyx characters**

In *S. gesnerioides*, each calyx rib ends in a tooth. Of ten collections flowering at the time of observation, six had 5 calyx teeth on all flowers examined. In three collections, the occasional calyx with 6 teeth was noted. The yellow-flowered, short internode, succulent type from Makgadikgadi (sheet 36) was the exception, with tooth number being 6 or 7. Calyx length across all collections was in the range of 3-6.5 mm from base to sinus with a tooth length of 1.5-4 mm.

**Floral morphology**

A number of floral characters were noted to show considerable variation between sites. Corolla color is generally light pink to mauve/lilac. At Makgadikgadi, Maun-Nata site 2, and Kanyu, however, pale yellow-flowered types were found. A yellow-flowered specimen had previously been collected at Otse, South-east District (*P. J. Mott 426*, University of Botswana Herbarium).

Length of the corolla tube for specimens examined was in the range of 7-10 mm. Dimensions of the corolla lobes, however, varied considerably. Largest flowers were found on plants with long internodes, e.g. Kanyu (sheet 26), with an upper lobe of 4 mm long, and three lower lobes between 4.5 and 8 mm, and on the collection south of Gumare (sheet 35), with an upper lobe of 3.5 mm and lower lobes 5-8 mm long. Elsewhere, upper lobes did not exceed 2.5 mm, while lower lobes were generally below 4 mm.

**Morphotypes of *Striga gesnerioides***

MUSSELMAN & PARKER (1983) reported host specificity in *S. gesnerioides* to be strongly correlated to the morphotype. A number of morphotypes with distinct combinations of stem morphology, internode length, flower color, and size can be recognized in Botswana and appear to be host-specific.

The following morphotypes occur :

A. Short internodes (2-5 mm), succulent stems 8-18 cm tall, with yellow flowers. Host : restricted to an *Ipomoea sp.*

B. Short internodes (2-11 mm), succulent stems 7.5-13 cm tall, with light-pink to deep-purple flowers. Host : *Indigofera sp.* and *Pteridiscus sp.*

C. Medium internodes (4-25 mm), non-succulent stems 7-24.5 cm tall, with light-pink flowers, lower lobes 2-3.5 mm long. Host : *Tephrosia sp.*

D. Long internodes (6-32 mm), non-succulent stems, occasionally red pigmented, large light-pink flowers, lower lobes 5-8 mm long. Host : *Rhynchosia*, *Tephrosia*, and an undetermined species of *Convolvulaceae*.

**STRIGA BILABIATA** (Thunb.) Kuntze

*S. bilabiata* failed to grow in the trials hence no material was available for discerning the host-range and life cycle. After-ripening is necessary in *S. asiatica* for roughly six months before seeds will germinate. It is possible that *S. bilabiata* may also require a period of after-ripening perhaps of greater duration than that for *S. asiatica* since the seed used in the trial had been collected only seven months earlier.

In fact, *S. bilabiata* did germinate in two pots of maize. The maize was growing very poorly and the pots were tipped so that the roots could be examined before they rotted. In two cases small haustoria were found each with an etiolated shoot.

Morphological observations on this species are restricted to plants collected at the Kanyu site parasitising *Schmidtia pappophoroides*. In his treatment of the *S. bilabiata* complex in West Africa, HEPPER (1960) designated five sub-species on a combination of diagnostic characters. The Kanyu specimens, with obtusely square stems, linear to elliptic bracts, subulate calyx teeth, and a close inflorescence, appear to fit quite well into *S. bilabiata* subsp. *bilabiata*. Comparison of our collection with specimens from Botswana in Kew seen by HEPPER, e.g. from Lobatse (*Tapscott*) and Okavango valley (*Lugard 270*) should be undertaken. Stem heights of up to 42 cm means that the Kanyu material is taller than the majority of the 243 *S. bilabiata* specimens measured by HEPPER. The maximum frequency in the group was in the 16-20 cm grouping. The Kanyu material consistently has 5 calyx ribs, with each rib terminating in a calyx tooth. Hairs on the stem are ascending, and the corolla tube is conspicuously hairy, keying out to *S. bilabiata* with no difficulty, using the key for *Striga* in East Africa (HEPPER, 1984). Divergent leaves of 15-21 mm which are not reduced, conspicuously hairy corollas on plants with 4 to 5 ribs or nerves, each ending in a calyx tooth likewise keys down to *S. bilabiata* in MUSSELMAN & HEPPER (1985) for Sudan witchweeds.

## RELIABILITY OF TAXONOMIC CHARACTERS

Keys to *Striga* often use calyx rib number as the primary determinant, as well as size of calyx and corolla tube, flower color, bract size, pubescence, and inflorescence (WETTSTEIN, 1893; HUTCHINSON & DALZIEL, 1963; MUSSELMAN & HEPPER, 1985). WETTSTEIN's infrageneric classification of *Striga* into the *Pentapleureae*, with five calyx ribs each terminating a lobe, and the *Polypleureae*, with ten or more ribs, alternately terminating a lobe, could not be strictly applied to our specimens. Such variability in calyx rib number has been discussed by MUSSELMAN in reference to findings in Sudan and other African countries (MUSSELMAN & AYENSU, 1984). The use of this character in keys should be modified to include the different arrangements of calyx ribs. Corollas are also variable among *Striga* species. The number open at a time per inflorescence branch ranges from 1 to 5 for all three species examined. Furthermore, lobe size and pigmentation in *S. asiatica* were variable. Flowers, therefore, also need to be described in terms of a range of findings.

Characteristics relating to pubescence and overall plant architecture, however, appear to be more consistent.

## FLORAL SYNDROME AND MODES OF POLLINATION OF STRIGA SPECIES

### *Striga asiatica*

Flowering commences 2-4 weeks after emergence of the shoot. Nodes at the top of the main stem develop pairs of buds, although it is not uncommon to find a node producing one flower and one branch, particularly in the first nodes where flowering occurs. Once the corolla is visible from the calyx, it elongates for one or two days before opening. Flowers persist for two days. The number of flowers open at a time per inflorescence branch is 2-5, rather than two only, as reported for plants in Sudan (MUSSELMAN & HEPPER, 1985). Floral development is always acropetal as the stem elongates. Up to 21 nodes on a single main stem were recorded to produce flowers in trials. Flowering on branches begins roughly 7-10 days later than the main stem, in the highest branches first, and then progressing to the lower branches. Up to 16 nodes on a single branch have been recorded to flower in trials. Flowering lasts for 3-4 weeks, but the final few flowers are smaller, malformed, and pale. The final buds elongate but do not open. Floral lobes, measuring from 2-5 mm wide and 5-8 mm long, may be narrow and spreading or wide and overlapping. In rare cases, four, rather than three, lobes will make up the lower lip, generally, with one far smaller than the remaining three. Emargination of the upper lobe may be marked or undetectable.

The androecium is epipetalous and moves forward with the tube during elongation. The style also elongates, and when the flower opens, the stigma is parallel with the anthers. Prior to opening, the corolla tube bends away from the stem at an angle of 45-90°. The bend flattens out the tube slightly in the area where pollination occurs. Hairs on the inner surface of the corolla tube point outwards. These physical features serve to assure autogamy, along with the sticky consistency of the pollen, which forms a plug over the stigmatic surface (MUSSELMAN & RICHES, 1985). Not only is autogamy assured, therefore, but pollen of other species is blocked. After the corolla tube whithers, the style and the pollen plug persist. Flowers open following anthesis before mid-morning.

Despite the fact that *S. asiatica* is autogamous, it bears features of an entomophilous out-crosser. It has showy flowers that may persist for two days, and the entire plant flowers for several weeks.

### *Striga gesnerioides*

Flowering commences 7-10 days after emergence in this *Striga* species and floral progression is similar to that in *S. asiatica.* Up to 16 nodes on a single plant were recorded to produce flowers in trials. Flowers persist for two days or more.

The corolla tubes arch away from the stem at an angle of 40-50°. The inside of the tube is densely pubescent, with the hairs pointing upward. At 9:00 am, anthers in new buds have not shed pollen, while those in buds in the process of opening have shed pollen. Furthermore, flowering in *S. gesnerioides* is not highly conspicuous or persistent. The evidence, therefore, supports a strongly autogamous mode of pollination.

### *Striga bilabiata*

The following observations were made on the field collection from Kanyu.

The flower has two lobes. The upper lobe is strongly recurved, about 4 mm in width. The lower lobe appears like a fused mass of the three in *S. asiatica*, with two emarginations half the length of the lobe. One to five flowers are open at a time per inflorescence branch. Floral progression appears the same as for *S. asiatica.* The corolla tube has a fairly wide opening and is arched, but not sharply bent, away from the stem.

There are no previous reports of the mode of pollination in *S. bilabiata*. Our studies indicate that this species is autogamous. During early evening, the corolla, as yet unopened, extends beyond the calyx teeth. At this stage the corolla tube is approximately 7.75 mm from base to the orifice of the tube. Dissections indicated that in this pre-anthesis position, the papillate surface on the adaxial side of the stigma is appressed to the stamens. Following sunrise, the corolla has extended a further 1 mm and a sticky mass of pollen has been shed — stamens, by this stage, moving to 0.5 mm above the stigma. Corolla and style elongation then proceeds a further 1 mm. The two upper dehisced stamens are clearly visible approximately 1 mm down the throat of the corolla and no hairs occlude the orifice as with *S. gesnerioides* and *S. asiatica*.

Two further structural feature seem to ensure autogamy. Firstly, the inner surface of the corolla at the position of the stamens at dehiscence is hairy. Pollen is trapped on these hairs. Secondly, before opening, the tube becomes compressed, ensuring pollen contact with the elongating style.

Morphological features of a possible vestigial entomophilous pollination syndrome are the production of copious, very sweet nectar, showy flowers, and a long period of flowering per plant. During observations of *S. bilabiata* in the field, floral visitors were not conspicuous. Further evidence of autogamy is the almost 100 % rate of capsule production.

## EXPERIMENTAL CROSSES

Reciprocal crosses between *S. asiatica* and *S. gesnerioides* (Table 1) did not succeed in producing seed. However, seed production did occur for all cross-pollinations within *S. asiatica*, whether between shoots in different pots or in the same pot, or between different flowers on the same shoot. Capsule enlargement was obvious within seven days. It appears, then, that *S. asiatica* and *S. gesnerioides* are not interfertile. There is, therefore, a genetic barrier to interfertility, as well as strong autogamy.

Cross-pollinations attempted between *S. bilabiata* and *S. asiatica* or *S. gesnerioides* (Table 2) were also unsuccessful. No capsules were formed. Fertility between these species can not be ruled out, however, until unilateral interfertility with *S. bilabiata* as the pistillate parent is examined.

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## APPENDIX

## SEED ACCESSIONS USED IN POT CULTURES

***Striga asiatica***

SA1 Collected in 1985 from Sebele Agricultural Research Station in the south-east district of Botswana. Host : sorghum.

SA2 Collected in 1985 from Ramatlabaki in the Kgatleng district of southern Botswana. Host : sorghum.

SA3 Collected in 1985 from Mahalapye in the central district of Botswana. Host : sorghum.

SA4 Collected in 1985 from Marapong in the north-east district of Botswana. Host : sorghum.

SA9 Collected in 1980 from Ntoro Farm, Matabeleng lands, in the Kgatleng district of southern Botswana. Host : sorghum.

SA10 Collected in 1980 from Ntoro. Host : maize.

SA11 Collected in 1980 from Thlaype Lands Kgateng District. Host : pearl millet.

***Striga bilabiata***

SB1 Collected in 1985 from Nxai Pan (Kanyu flats) in Ngamiland in northern Botswana. Host : *Schmidtia pappophoroides.*

***Striga gesnerioides***

SG1 Collected in 1985 from Jwaneng in the central district of Botswana. Host : *Indigofera sp.* Short internodes.

SG2 Collected in 1985 from Nxai Pan (Kanyu flats) in Ngamiland, northern Botswana. Host : *Tephrosia sp.* Short internodes.

SG3 Collected in 1985 from Nxai Pan in Ngamiland. Host : *Tephrosia sp.* Long internodes.

SG4 Collected in 1980 from Kutse in the Kweneng district. Host : unknown. Short internodes.

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